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Jennings, D. J., Elwood, R. W., Carlin, C. M., Hayden, T. J., & Gammell, M. P. (2012). Vocal rate as an assessment process during fallow deer contests. *Behavioural Processes*, 91(2), 152-158.
<https://doi.org/10.1016/j.beproc.2012.07.003>

Published in:
Behavioural Processes

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
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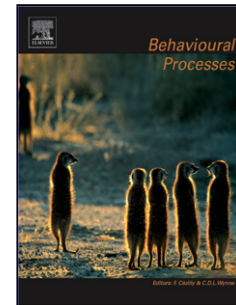
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Accepted Manuscript

Title: Vocal rate as an assessment process during fallow deer contests

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PII: S0376-6357(12)00148-9
DOI: doi:10.1016/j.beproc.2012.07.003
Reference: BEPROC 2515

To appear in: *Behavioural Processes*

Received date: 23-4-2012
Revised date: 10-7-2012
Accepted date: 10-7-2012

Please cite this article as: Jennings, D.J., Elwood, R.W., Carlin, C.M., Hayden, T.J., Gammell, M.P., Vocal rate as an assessment process during fallow deer contests, *Behavioural Processes* (2010), doi:10.1016/j.beproc.2012.07.003

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Vocal rate as an assessment process during fallow deer contests

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Abstract

Two types of model propose that strategic decisions during contests are determined either by (i) a mutual-assessment process or (ii) a self-assessment process. Vocal signals are thought to convey information about the competitive abilities of individuals, the ultimate function of which is a reduction in costs associated with fighting consistent with the principle of mutual assessment. Nevertheless, the limited evidence that male ungulates engage in mutual assessment of vocal rates during dyadic contests has been questioned. Therefore, we examined the vocal rates of winners and losers during escalated dyadic contests between male fallow deer in order to further inform on this issue. Our results showed that winners and losers did not differ in vocal rate. The best model fit that accounted for individual vocal rates included a preponderance of factors related to the opponent indicating that contestants were attending to their opponent during fights. Vocal rate was, therefore, dependent on estimates of opponent quality without reference to self, supporting an 'opponent-only' rather than a mutual assessment process.

Keywords: Vocal rate, resource holding potential, fighting, self- and mutual-assessment, 'opponent-only' assessment

42 Introduction

43 Within the field of animal competition, a single theoretical account that accurately describes the
 44 strategic decisions made by animals during dyadic contests for resources remains somewhat elusive.
 45 While contestants typically use information concerning the value of the disputed resource and
 46 adjust their tactics in accordance with this estimate (e.g. Goubault et al. 2007; Arnott & Elwood
 47 2008), there is disagreement concerning the information gained about opponent fighting ability
 48 (Arnott & Elwood 2009). Models developed for this latter purpose can broadly be placed within two
 49 classes that differ fundamentally in how they describe the assessment process: one class emphasises
 50 the role of self-assessment whereas the other emphasises a process of mutual-assessment (Taylor &
 51 Elwood 2003; see Briffa & Sneddon 2010 for a review).

52 Under a self-assessment process no information is gathered about the quality of an
 53 opponent. Both contestants are expected to fight until they reach some cost threshold that the
 54 individual is willing to pay (e.g. time, energy or damage). This class of model assumes that there will
 55 be no difference in the repetition rate of aggressive actions between the opponents although rates
 56 are permitted to escalate and de-escalate over the duration of the contest (Briffa & Elwood 2009,
 57 Table 1). Therefore, under a self-assessment process, contestants illustrate their quality by matching
 58 action rates with their opponent (Briffa & Sneddon 2010). Whichever contestant reaches its cost
 59 threshold first will give up at that point and its opponent will either retain, or take control of the
 60 resource (e.g. energetic war of attrition: Payne and Pagel 1996; cumulative assessment model:
 61 Payne 1998). In line with predictions regarding competitor behaviour, there is considerable empirical
 62 evidence for self-assessment as a form of contest strategy in a variety of different species (e.g. fallow
 63 deer: Jennings et al. 2004, 2005a; amphipod crustacean: Prenter et al. 2006; house cricket: Briffa
 64 2008; jumping spider: Elias et al. 2008).

65 Models of mutual-assessment propose that each opponent gathers information about the
 66 other contestant and compares that with its assessment of its own ability or quality. One influential

67 account, the sequential assessment model (SAM, Enquist & Leimar 1983), is explicit as to how
 68 animals monitor the aggressive displays given by their opponent and, therefore, how opponent
 69 display rates affect the decisions that animals make during contests (Enquist et al. 1990). The model
 70 assumes that when two contestants enter into a contest that their respective estimate of each
 71 other's quality will be poor at the beginning; however, by repeated sampling of opponent display
 72 rates this error in assessment is reduced. Consequently, rather than continue until a maximum cost
 73 threshold is reached, a contestant is predicted to persist only until it determines that it will not
 74 succeed in winning and elects to abandon the interaction. Therefore, contest duration should be
 75 positively related to loser quality but negatively related to winner quality (Taylor & Elwood 2003).
 76 We would also expect a negative relationship between difference in opponent quality and contest
 77 duration (Enquist & Leimar 1983; Enquist et al. 1990) although this is not a diagnostic feature of
 78 mutual assessment (Taylor & Elwood 2003). A critical feature of the mutual assessment process is
 79 that information quality must be reliable and not easily faked; therefore, signals employed during
 80 dyadic contests are expected to be costly to produce (Maynard Smith & Harper 2003).

81 It has been shown that males of numerous species engage in vocal displays that apparently
 82 convey information about their quality and/or aggressive intent (Andersson 1994). For example,
 83 male songbirds' aggressive intent can be determined by song matching or countersinging between
 84 the prospective opponents (Todt & Naguib 2000). Similarly, interactions between males of several
 85 anuran species involve an increase in individual vocal rates in response to a potential rival (e.g.
 86 Wagner 1989; Bosch & Marquez 1996). When male ungulates are vocal (but not otherwise
 87 interacting) there can be a tendency towards very high vocal rates (e.g. McElligott & Hayden 1999)
 88 relative to the rates observed when males are engaged in multi-male vocal contests (e.g. Wolff
 89 1998) or in pairwise interactions (e.g. Clutton-Brock & Albon 1979). In the latter case it has been
 90 argued that high vocal rates inhibit vocal exchanges between individuals because one member of
 91 the interacting dyad is actively prevented from vocalizing (e.g. Clutton-Brock & Albon 1979; Clutton-
 92 Brock et al. 1988; Komers et al. 1997). This observation placed in theoretical terms suggests that a

mutual assessment process, which relies on cooperation between contestants, might hold. If this is the case, it seems unlikely that high vocal rates would facilitate mutual assessment of opponent quality in many of the contexts in which vocal behaviour has been observed (e.g. Clutton-Brock et al. 1988; McElligott & Hayden 1999; see Enquist & Leimar 1983; Enquist et al. 1990).

A finding that has been cited in support of evidence for mutual assessment is the presence of a winner-loser disparity during vocal contests in red deer (Clutton-Brock & Albon 1979; Enquist & Leimar 1983); however, another key feature of mutual assessment was not, i.e. a stable rate of repetition over contest duration (Payne & Pagel 1997; Payne 1998; Briffa & Elwood 2009).

Nevertheless, there is potentially a complex interplay between the context in which vocalizations are emitted and the form of assessment process being employed. For example, high repetition rates could support a self-assessment process subject to certain constraints; for example, matched rates where more than one male is vocal (Mesterton-Gibbons et al. 1996; Payne 1998; Briffa & Elwood 2009; see for example Wolff 1998). Alternatively, if only a single male is vocal, a form of 'opponent-only' process but not mutual assessment might be applicable (Arnott & Elwood 2009). Therefore, while there is most likely some form of on-going assessment process related to vocal rates in ungulates, it is unclear what form that process takes and how this might be influenced by context.

The present study sought to investigate this issue by focussing on vocalizations emitted during a single defined context - the escalated contest. These contests involve the use of many different types of action that are potentially a source of information concerning opponent quality (Jennings et al. 2005a, 2010). However, the interaction between these actions and vocal behaviour have rarely been investigated (but see Logue et al. 2010); therefore, they could inform on any on-going assessment process. The present study addresses this issue. If a mutual assessment process is applicable to vocal rates during fallow deer contests then certain theoretical predictions must be met (Arnott & Elwood 2009). Specifically, vocal rate should be related to the competitive ability of the producer; therefore winners should out-produce losers and, furthermore, dominance rank

118 should be related to the vocal rate of both contestants. In keeping with mutual assessment, contest
119 behaviour should be related to the disparity in vocal rates between the winner and loser;
120 specifically, as winner quality increases relative to loser there should be a reduction in contest
121 action rates since the disparity in quality should become clear early in the contest (Enquist &
122 Leimar 1983; Enquist et al. 1990). If this is the case then contestants that are more closely matched
123 in terms of competitive ability will vocalise at a higher rate. Conversely, if a self-assessment process
124 is applicable then we would expect that contestants should match their vocal rates independent of
125 dominance rank (Payne 1998; Briffa & Elwood 2009; Arnott & Elwood 2009). The present study was
126 conducted to determine which of these alternative hypotheses best accounted for vocal rates during
127 escalated contests in the fallow deer.

128

128 Methods

129 Study site and population: This study was conducted over two consecutive rutting seasons (1996
130 and 1997) on a herd of free-ranging European fallow deer resident in the Phoenix Park – a large
131 enclosed city park consisting of 709 ha located at Dublin, Ireland (53° 22' N, 6° 21' W). The majority
132 of the park (80%) is open grassland with the remaining 20% covered by mixed woodland. Fawns are
133 tagged in each ear with unique colour/numbered tags shortly after birth in June and July each year.
134 Identification of mature males in the population is facilitated by a combination of ear tags, coat
135 colour and antler conformation.

136
137 Study System: The fallow deer is a seasonally breeding ungulate; the annual rut takes place from
138 mid to late October in the Northern hemisphere. From late September and through October mature
139 males show increasingly heightened levels of aggression with each other; there is an increasing
140 tendency to escalate to fighting in relation to the number of matings observed in the population
141 (Jennings et al. 2006, 2009). We addressed the function of groaning during contests that involved
142 fighting in the present study. These contests could start with antler engagement following an
143 approach by one male towards another or with a parallel walk that proceeded to antler contact
144 (Jennings et al. 2003). To provide a clearly defined context and opponent in which to examine vocal
145 rate as an assessment process, we recorded vocalizations from the point at which two males started
146 to interact (e.g. started to parallel walk) and until the loser terminated the contest. In order to
147 account for differences in contest duration we calculated winner and loser vocal behaviour as a rate
148 per minute score (number of groans / non-contact duration * 60). Because males do not vocalise
149 when in antler contact we excluded the duration that contestants spent with antlers locked when
150 calculating vocal rate per minute.

151 Fallow deer fights involve a range of aggressive actions, such as backward pushing, jump
152 clashing and retreats (e.g. Alvarez 1993; Jennings et al. 2004, 2005a,b). Backward pushing involves

one animal forcing his opponent backwards while their antlers are locked, and jump clashing involves one animal initiating antler contact by jumping towards his opponent with his antlers lowered (Alvarez 1993). Retreats did not involve attacking an opponent; here one animal slowly backed away from his opponent with lowered antlers so that antler contact was broken. Once antler contact was broken the opponent often raised his antlers and slowly followed the retreating male (Jennings et al. 2005b). These actions are related to contest success and inform on assessment processes (Jennings et al. 2005 a,b), therefore, the approach adopted here was to include these data in the statistical models. This permitted us to examine whether vocal rates were determined by the action rates of either the opponent or self. Fights were recorded on video tape and screened using the Observer video analysis system (Noldus Information Technology, Wageningen, The Netherlands). We calculated the rate of these additional variables: the rate of backward pushes, jump clashes and retreats (per minute: number of actions / contact duration * 60) for both contest winners and losers per fight using the duration that antlers were in contact.

Dominance ranking: Individual dominance ranks were calculated for each male in both years of the study using David's score (Gammell et al. 2003); we used all decisively resolved non-contact interactions recorded between mature males (4+ years) in that year to calculate dominance ranks. The two hierarchies are linear indicating that dominance relations between the males in both years were transitive (Jennings 2007). For pooled analyses involving dominance ranks, the David's scores were converted to ordinal ranks, the animal with the highest David's score in each year was assigned an ordinal rank of 1. Dominance rank provides a good measure of individual quality in the fallow deer and reliably correlates with mating success (e.g. Jennings et al. 2011).

Statistical analyses

We used generalized linear mixed models fitted with a restricted estimate maximum likelihood (REML) in the lme4 package for R (version 2.13.1). Because the dependent variables were transformed count data we used a Poisson distribution with Laplace parameter estimation for the models (Crawley 2007). Some individual males were recorded in more than one contest as a winner or loser and because vocal rate can change over the rut (e.g. Clutton-Brock et al. 1988, Table 4), we fitted the factor Day (calculated from the first day of October) within individual buck identity (winner and loser) as random effects to account for temporal pseudoreplication (Crawley 2007). There were 42 individual males recorded on video tape that competed in 51 escalated contests with antler contact (fighting) and where at least one competitor was vocal. In order to test the different predictions outlined in the Introduction we ran separate models to explain winner and loser vocal rates. In order to reduce the full model to the best model (Burnham & Anderson 2004), we iteratively removed fixed factors from each model based on the z value score (removing the smallest value first) and then conducted a likelihood ratio (LR) test where: $LR=2*[(\log\text{-likelihood of the best fitting model})-(\log\text{-likelihood of the worst fitting model})]$, the best fitting model having the highest log-likelihood score. The significance of the LR is evaluated against a chi-square distribution with degrees of freedom equal to the difference in the number of predictors between the two competing nested models. The statistical models used here analyse the effect of several independent variables on the dependent variable; therefore the graphs presented show the relative effect of the independent variable of interest on the dependent variable (thus taking the effect of all independent variables into account; Jennings 2012).

Results

The effect of contest action rate on groan rate

Winners and losers displayed similar rates of vocalizing over contest duration (Means = 3.8 and 5.2 per minute, SE \pm 0.8 and 0.9 respectively) and there was no difference in groan rate ($t = 0.65$, $p = 0.5$) and no effect of contest duration ($t = 1.17$, $p = 0.2$) and no outcome \times contest duration interaction ($t = -0.20$, $p = 0.8$). Within each model, both winner and loser groan rate were predicted by the opponent's groan rate (Table 1, Figure 1a and 1b). Winner vocal rate was predicted by both own and the loser's dominance rank (Table 1, Figure 2a and 2b); however, loser rate was not predicted by either own or winners rank. Winner vocal rate was negatively associated with backward push rate of the loser (Table 1, Figure 3a) and positively related to loser jump clash rate (Table 1, Figure 3b).

Loser vocal rate was negatively related to winner retreat rate (Table 1, Figure 4); no other fixed factors were significant contributors to the model. Simplifying the models was attained by removing the weakest fixed factors in order to determine the best (most parsimonious) model relative to the full model: four variables were removed from both the full winner and loser models. For the winner model: winner jump clash rate, backward push rate, retreat rate and loser retreat rate were removed without a significant effect on the model (LR = 6.78, $df = 4$, $p = 0.15$). Removal of a fifth fixed factor, loser backward push rate, resulted in a model with significantly less explanatory power than the full model (Full model: AIC = 147.14, log likelihood = -57.59; Reduced model: AIC = 150.02, log likelihood = -64.01; LR = 12.89, $df = 5$, $p = 0.025$). For the loser model: loser retreat rate, jump clash rate and winner backward push rate, jump clash rate were removed without a significant decline in explanatory power (LR = 2.32, $df = 4$, $p = 0.7$). The additional removal of winner dominance rank yielded a significant reduction in explanatory power (Full model: AIC = 158.05, log likelihood = -63.02; Reduced model: AIC = 161.58, log likelihood = -69.79; LR = 13.53, $df = 5$, $p = 0.019$).

225

226 Insert Table 1 about here

227 Insert Figures 1a and 1b, 2a and 2b, 3a and 3b, 4

228

229 Contest duration and dominance rank

230 The rank of the contest winner was related positively to contest duration ($t = 2.45$, $p = 0.01$), i.e. as
231 winner rank declined losers competed for longer (rank decreases with increasing number), but
232 there was no relationship between duration and loser dominance rank ($t = 0.67$, $p = 0.5$) and there
233 was no interaction ($t = -1.49$, $p = 0.1$, see Figure 5). There was no relationship between duration of
234 antler contact and winner rank ($t = 1.15$, $p = 0.3$) or loser rank ($t = 0.23$, $p = 0.8$) and no interaction (t
235 $= -1.15$, $p = 0.3$).

236

237 Insert Figure 5 about here

238

Discussion

Game theoretic models divide into two main categories that differ fundamentally with regard to the type of assessment process adopted by contestants. In order to differentiate between these forms of assessment process, a commonly employed approach focusses on contestants' rates of action repetition over contest duration (Briffa & Elwood 2009). Nevertheless, despite underlying theoretical differences, it is an expectation of both types of model that the assessment process adopted will continue until the loser determines that it cannot defeat its opponent, and abandons the contest (Enquist & Leimar 1983; Mesterton-Gibbons et al. 1996; Payne & Pagel 1996, 1997; Payne 1998). Escalated contests in ungulates are characterised by a range of offensive and defensive actions that can inform on the strategic decisions adopted by contestants (Alvarez 1993; Clutton-Brock et al. 1979; Jennings et al. 2003, 2004, 2005a,b; Jennings 2012); however, despite potentially shedding light on this process, vocal repetition rates have received comparatively little attention (but see Clutton-Brock & Albon 1979). Moreover, because contests are energetically costly to the competitors (Briffa & Sneddon 2007), vocal rate could provide an accurate index of current rather than overall quality (e.g. dominance rank: Jennings et al. 2010, 2011). The present study addressed these issues; specifically, we investigated the function of vocal rate within the context of escalated contests and asked whether it corresponded with a mutual assessment process. Such an approach permitted us to test predictions derived from game theoretic models of contest behaviour, specifically that individuals employ mutual assessment of opponent quality during contests (Enquist & Leimar 1983; Payne & Pagel 1996, 1997; Payne 1998).

As noted above, individual vocal rates in male ungulates appear to be influenced by context. It has been noted that very high rates have been recorded when vocal males are in proximity to each other but not obviously engaged in agonistic interactions (e.g. McElligott & Hayden 1999), relative to vocal rates during dyadic contests (e.g. Clutton-Brock & Albon 1979; Wolff 1998). In the present study, the vocal rate of this population of deer approximated that of red deer engaged in dyadic

competition; therefore, by reference to the parameters established by Clutton-Brock and Albon (1979), vocal rates in this population appear to fall into a general optimum range that permits an exchange of information. We note that the data reported by Clutton-Brock and Albon (1979) are derived from interactions that precede antler contact whereas the present study takes its data from interactions that have escalated to contact. However, this discrepancy is not relevant in theoretical terms; only the SAM anticipates phases of escalating intensity; however, contest actions are permissible over all phases subject to the models theoretical constraints (Enquist & Leimar 1983; Enquist et al. 1990; Koops & Grant 1993 but see Hsu et al 2008). Nevertheless, the question as to whether red deer vocal rates during the pre-antler contact phase support a mutual assessment process has been challenged. The SAM predicts that both competitors should signal at a constant rate in order to facilitate the assessment process and this core prediction concerning repetition rate stability was not met (Payne 1998). Furthermore, it is important to note that evidence for vocal exchanges is not in itself evidence for mutual assessment; self-assessment models require monitoring of opponent action rates and because this requires matching of action rates they can comfortably account for such patterns of vocal exchange (Arnott & Elwood 2009; Briffa & Elwood 2009). We note that there is evidence of such matching in the present study.

Escalated contests generally involve many different forms of aggressive action (Hardy & Briffa in press); however, the relationship between contest actions and acoustic behaviour has rarely been investigated (but see Logue et al. 2010). Moreover, during fights, energetic costs are expected to increase as a consequence of an increase in the number of repetitions of an action or suite of actions (Briffa & Sneddon 2007). The production of vocalisations is thought to be costly (e.g. Oberweger & Goller 2001) and it is possible, therefore, that vocal rates might be affected by the current RHP of each contestant. However, there is inconsistent evidence to support this point; for example, when contestants remain silent there is a greater level of aggression than contests where males emitted acoustic signals (Logue et al. 2010) while the reverse has also been shown (e.g. Bartoš et al. 2007). Our results, suggest that vocal rate is unrelated to contest cost in terms of attacking

contest actions: the best model fits indicated that in both instances only slight support for the idea that attacking actions are positively related to vocal rate.

Under a mutual assessment process contest winners are expected to out-produce their opponent while holding vocal rates consistent over time (Enquist & Leimar 1983). This was not the case; winners did not out-produce losers and although vocal rates did not differ over contest duration, this aspect of repetition rate can be accounted for by a self-assessment process (Briffa & Elwood 2009). Therefore, consistent with one theoretical interpretation of red deer vocal contests (e.g. Payne 1998) a preliminary interpretation of repetition rates in this study do not support a mutual assessment process. However, during contests, vocal rate is expected to be related to resource holding potential of the producer (RHP: Parker 1974; Enquist & Leimar 1983, see Clutton-Brock & Albon 1979; Wolff 1998); therefore, we expect that vocal rate should be related to individual dominance rank. This was the case for winners but not losers (Table 1), although a simplification of the models that reduced the number of fixed factors indicated that winner and loser rank was an important factor in determining winner and loser vocal rates. Based on this somewhat restricted view of the data, i.e. focussing simply on the evidence for altering vocal rate based on both self and opponent dominance rank, our results show support for a mutual assessment process (Enquist & Leimar 1983; Payne 1998).

Examination of the full winner model shows that five of the nine fixed explanatory variables contributed significantly to the model; subsequent iterative removal of the four weaker factors indicated that these five factors should be retained in the best model (Burnham & Anderson 2004). With the exception of winner dominance rank, the remaining variables related to loser contest action rates and dominance rank. Under self-assessment we would expect winner vocal rate to be related to winner contest actions rates including dominance. From a theoretical perspective attending to the rate of behavioural actions of an opponent rather than the difference in rates falls outside predictions made by current models – both self- and mutual-assessment - and suggests an

“opponent-only” rather than mutual-assessment process (Arnott & Elwood 2009). The effect of action rate on loser vocal rate was more equivocal; in addition to the rank of both opponents, two winner factors and a single loser factor were retained in the best model while two winner and two loser variables were excluded. This suggests that there is some evidence to support an opponent-only assessment process. To further examine this possibility we regressed contestant dominance rank against contest duration. Only winner rank was related to duration: as winner rank, (i.e. quality) declined there was an increase in contest duration. Therefore, losers were sensitive to winner rank without reference to their own rank, which is consistent with an opponent-only assessment process. Perhaps because such predictions are not encompassed within traditional models there has been little attempt to formally investigate opponent-only assessment either as a contest strategy or to define it within a theoretical model. However, the present findings add to a number of empirical studies that demonstrate opponent-only assessment in insects (e.g. Rillich et al. 2007) and fish (Prenter et al. 2008; Reddon et al. 2011; reviewed by Arnott & Elwood 2009).

In conclusion, we have found that vocal rate during fallow deer contests do not conform to the theoretical prediction of either a self or a mutual assessment process. Rather, our results suggest that it is the action rate of the opponent during contests that is central to determining both winner and loser vocal rates. For both contestants it was evident that vocal rate was influenced by the motivation or willingness of their opponent to invest in the contest (see also Rillich et al. 2007; Reddon et al. 2011). Since methods were proposed to objectively discriminate modes of assessment in contests (see for example Briffa & Elwood 2009; Taylor and Elwood 2003), there have been a number of studies that indicate opponent-only assessment (see above) or no assessment at all (e.g. Reichert & Gerhardt 2011). The present study adds to these accounts in contradicting the pervasive view that animal contests are settled by a process of mutual assessment. Nevertheless, it still remains to be established whether such a process governs vocal behaviour over the range of contexts in which vocalizations occur.

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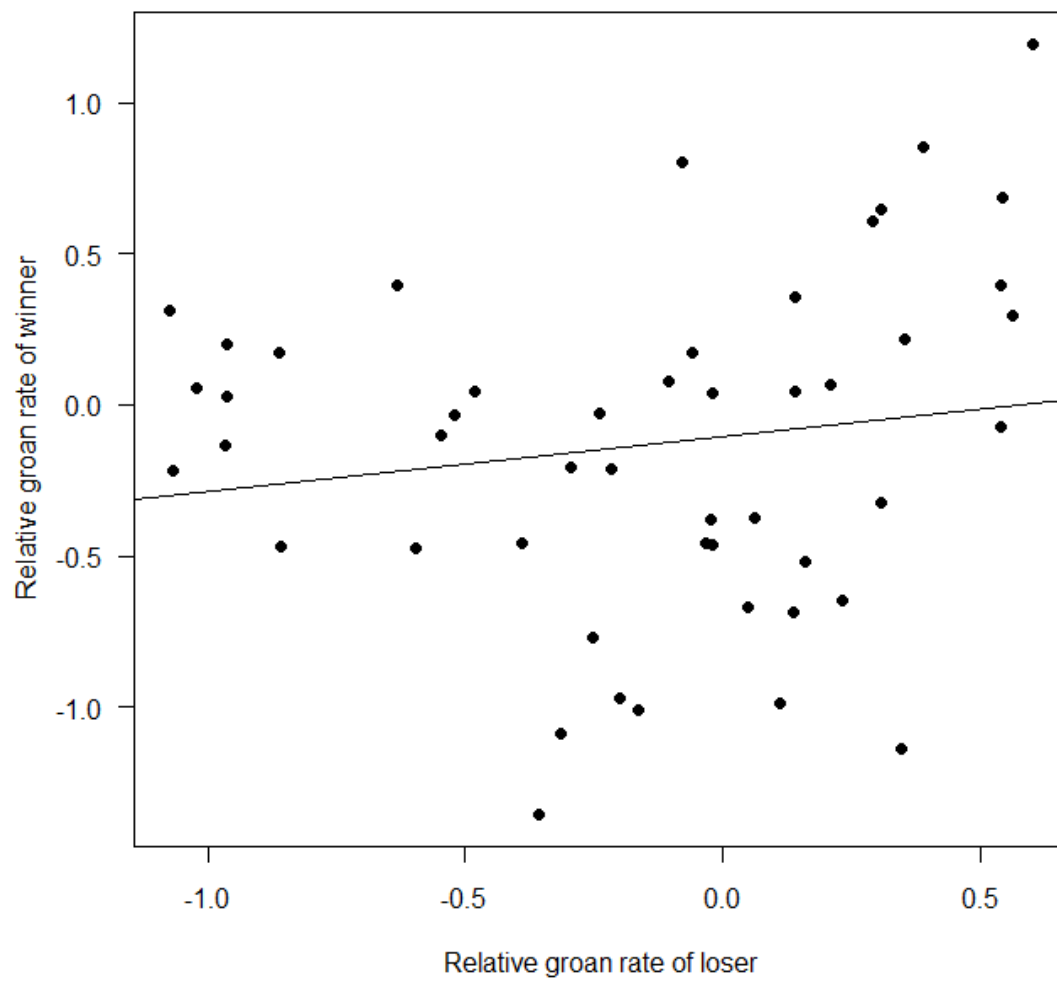
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- Figure 3. The relationship between winner vocal rate and loser contest actions rates. Panel A shows the relationship between winner vocal rate and loser backward push rate. Panel B shows the relationship between vocal rate and loser jump clash rate.
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479 Figure 1a

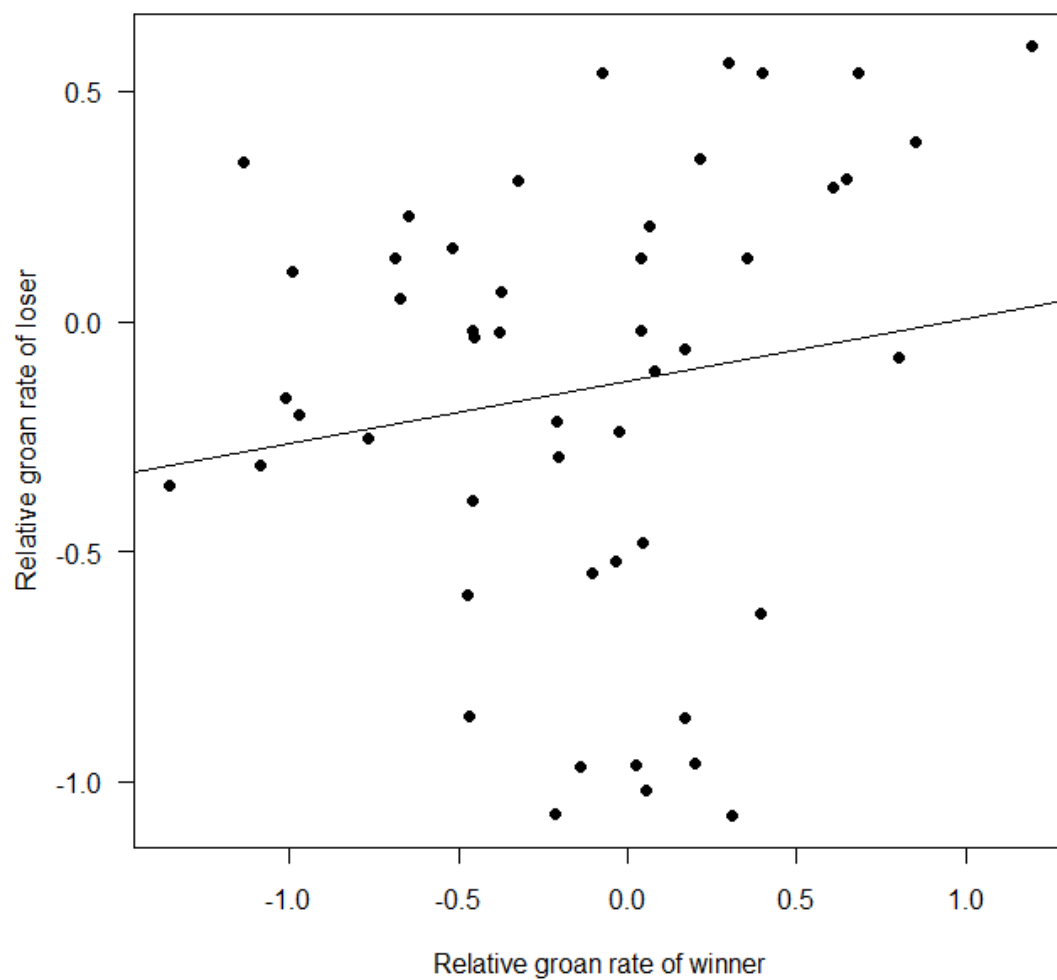


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482 Figure 1b



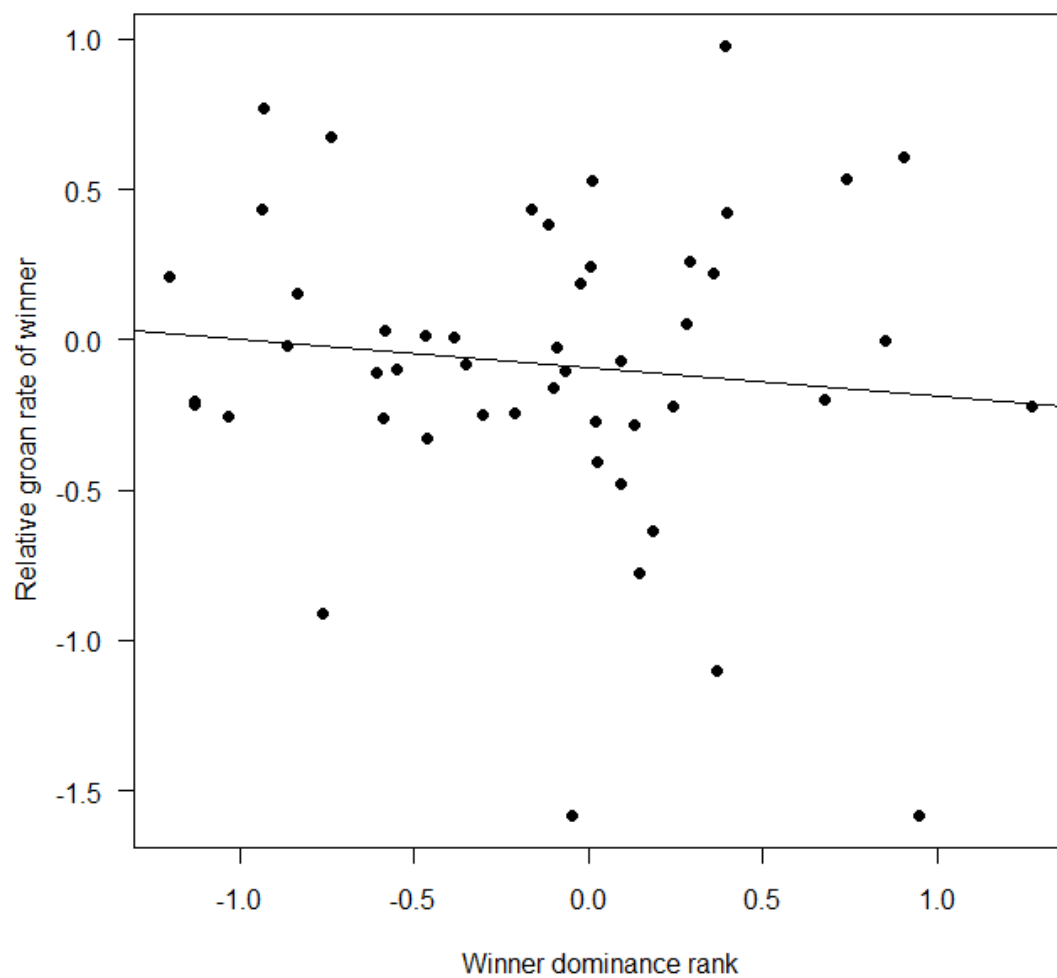
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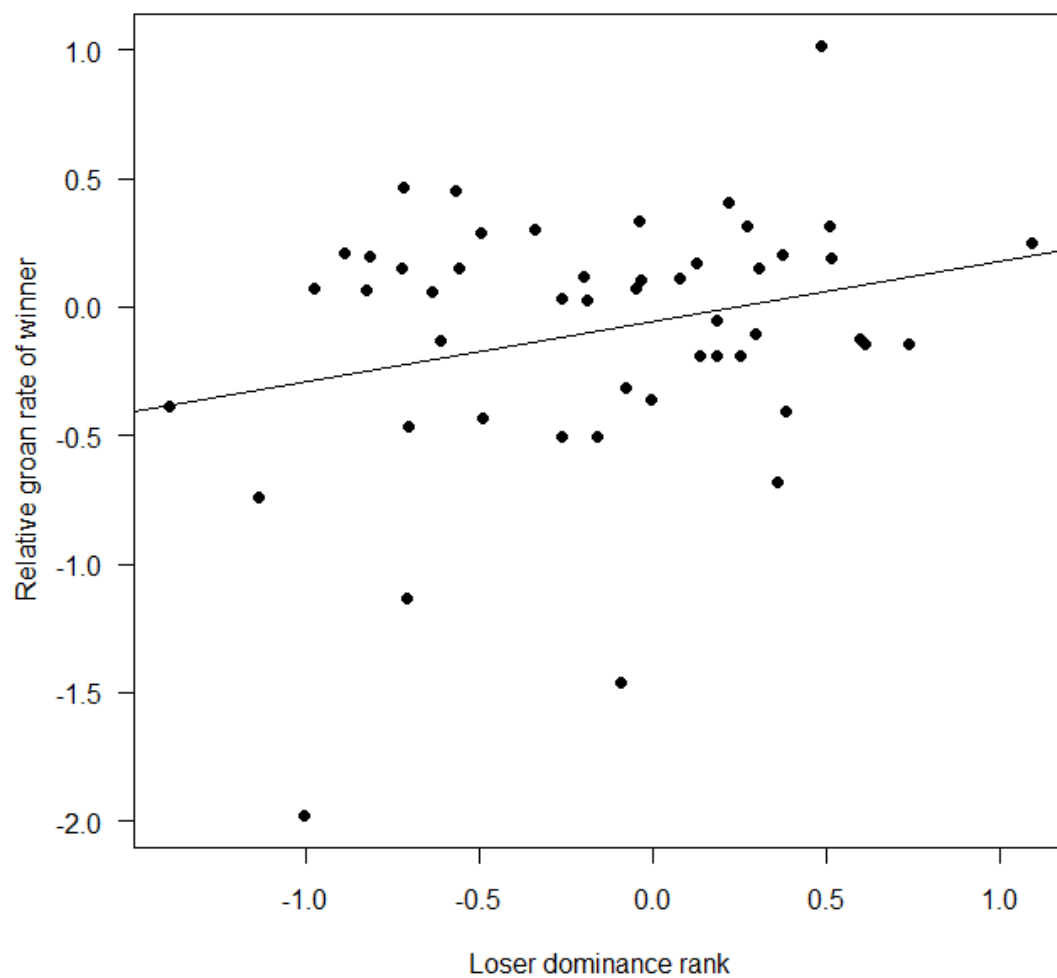


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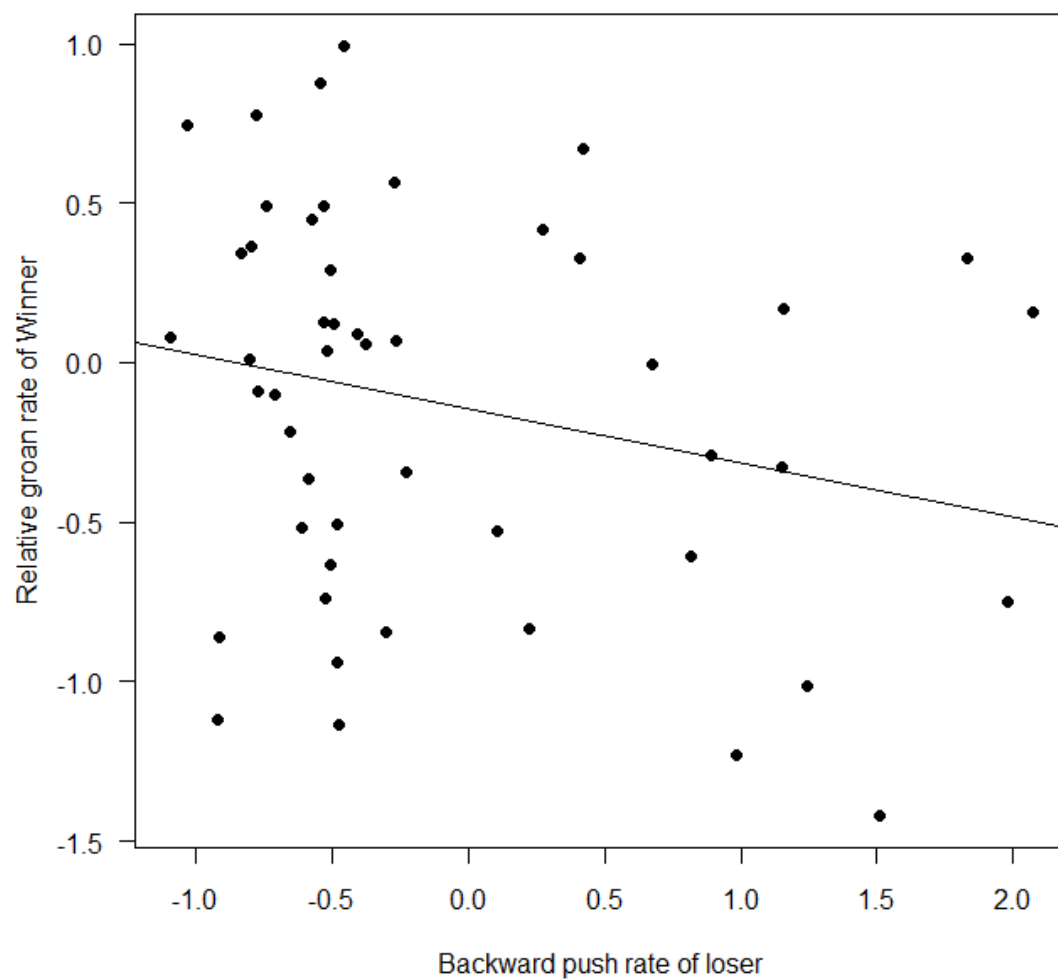
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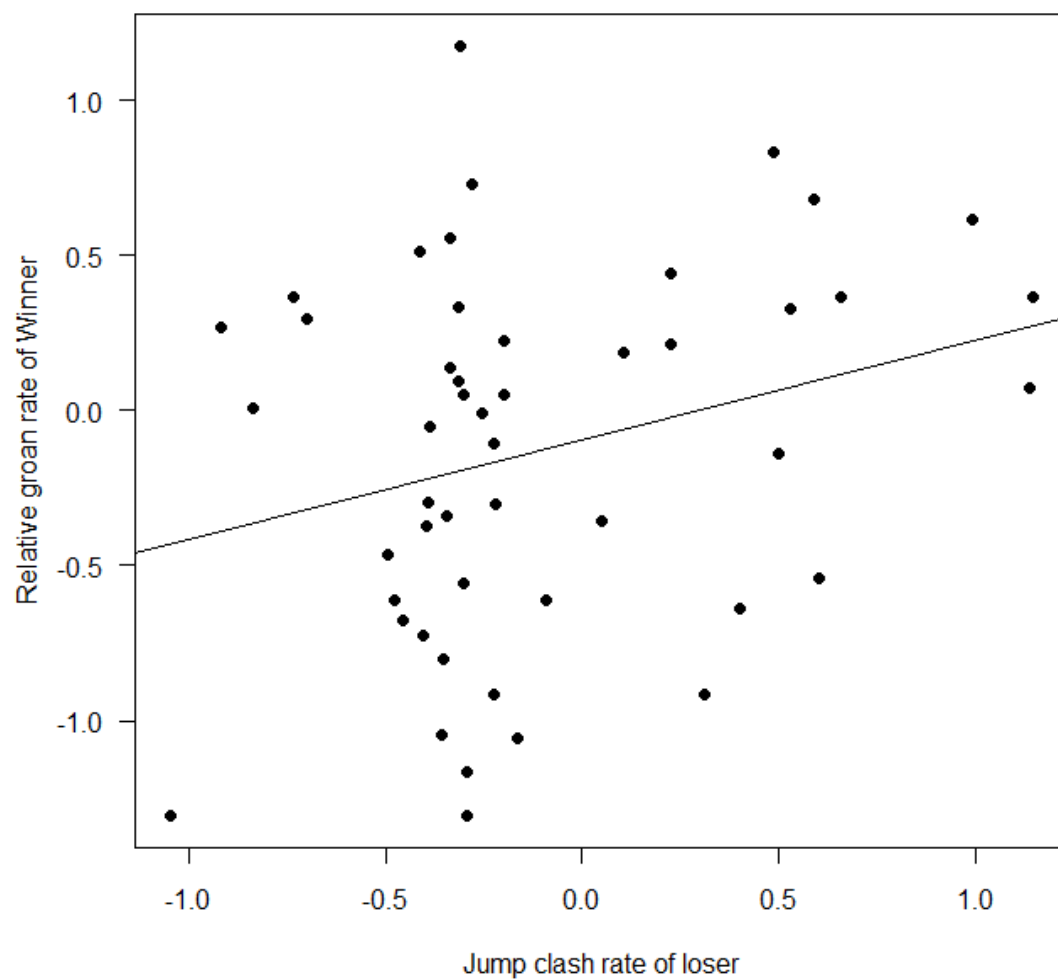


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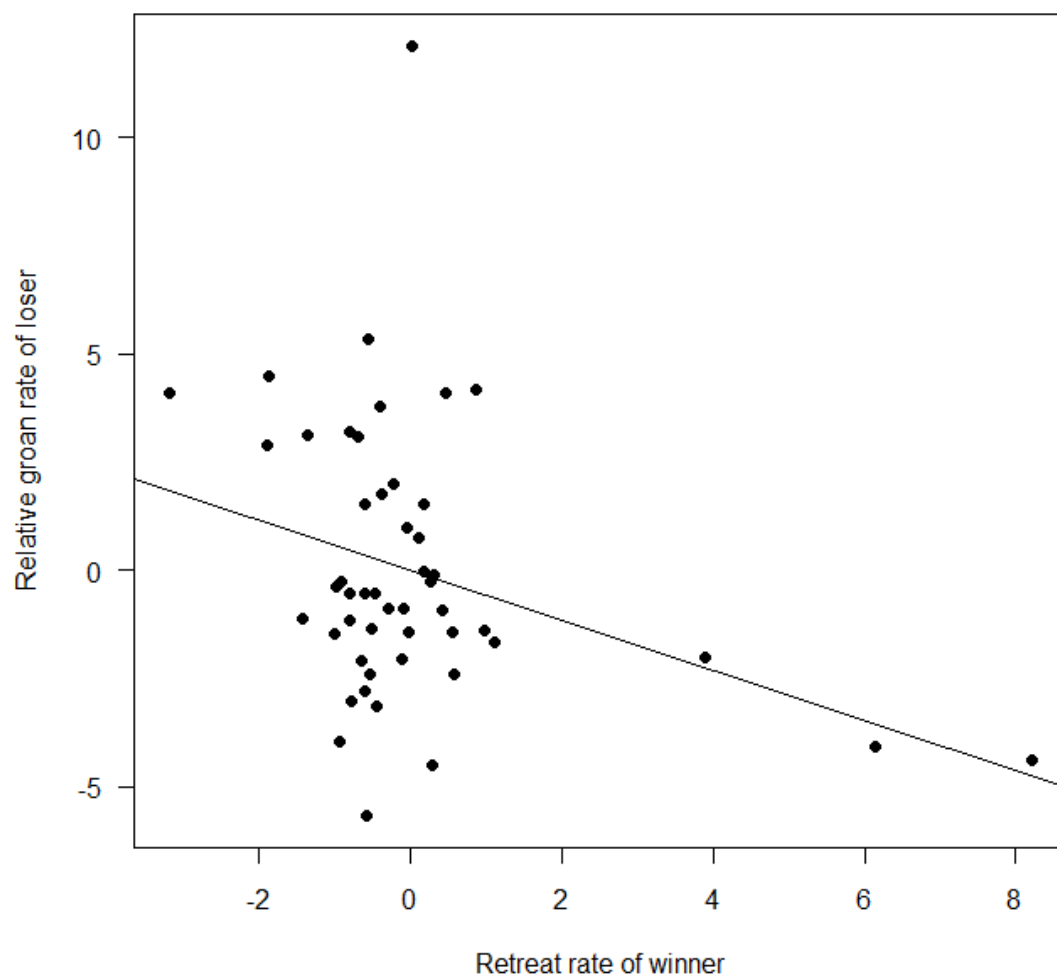


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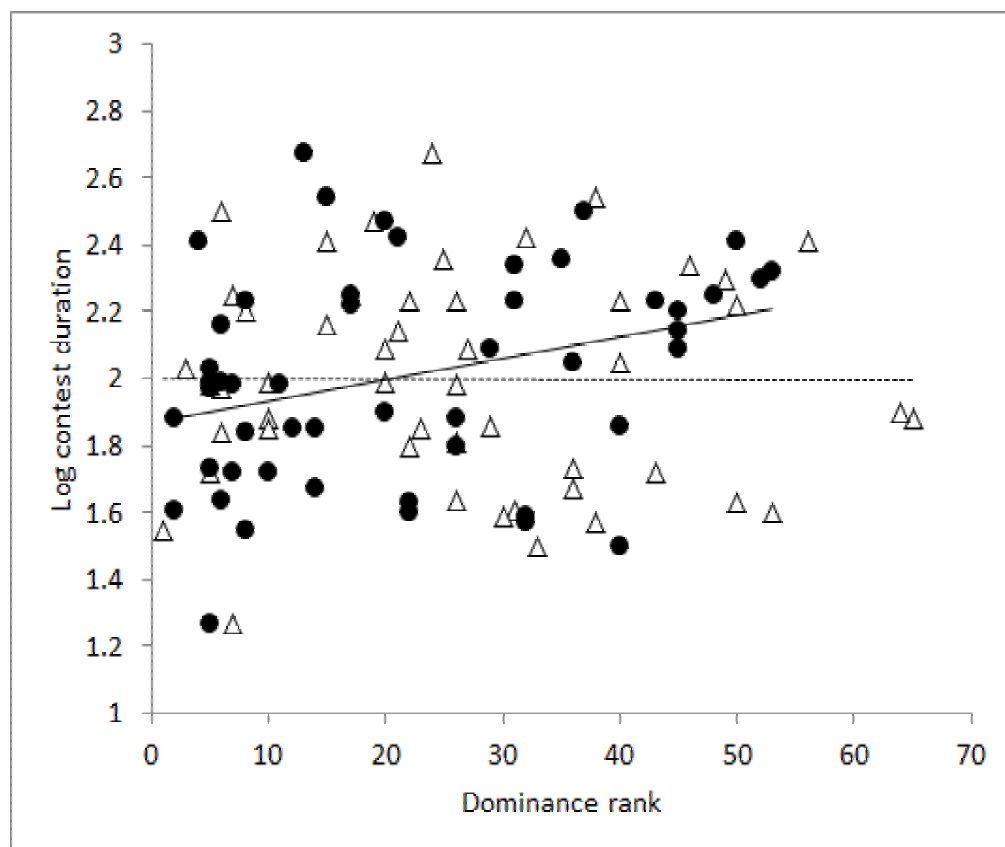
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501 Figure 5

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1 Table 1. Two generalised linear mixed models describing the contribution of nine fixed factors to winner and loser groan rate.

Fixed effects	Winner vocal rate	Estimate	SE	Loser vocal rate	Estimate	SE
Intercept	$z = 0.38, p = 0.7$			$z = 2.76, p = .006$	1.22	0.44
Opponent groan rate	$z = 3.19, p = 0.001$	0.07	0.02	$z = 2.00, p = 0.048$	0.07	0.03
Winner dominance rank	$z = -3.80, p = 0.002$	-0.04	0.01	$z = -0.85, p = 0.4$	-0.01	0.01
Loser dominance rank	$z = 3.19, p = 0.001$	0.04	0.01	$z = -1.05, p = 0.3$	-0.01	0.01
Winner backward push rate	$z = 1.01, p = 0.3$	0.05	0.05	$z = 0.304, p = 0.8$	0.02	0.05
Loser backward push rate	$z = -3.01, p = 0.003$	-0.42	0.14	$z = 1.64, p = 0.1$	0.20	0.12
Winner jump clash rate	$z = -1.00, p = 0.3$	-0.04	0.04	$z = 0.62, p = 0.5$	0.03	0.04
Loser jump clash rate	$z = 3.14, p = 0.002$	0.28	0.09	$z = -0.300, p = 0.8$	-0.03	0.11
Winner retreat rate	$z = 1.64, p = 0.1$	0.14	0.08	$z = -2.25, p = 0.02$	-0.39	0.17
Loser retreat rate	$z = -1.38, p = 0.2$	-0.03	0.02	$z = -0.11, p = 0.9$	-0.001	0.01

2 Winner rate model. AIC = 147.1, log likelihood = -57.57; Loser rate model. AIC = 158, log likelihood = -63.02.

3 Highlights

- 4 1. Investigates the relationship between vocal rate and assessment during escalated contests
- 5 2. Examines the role of contest behaviour of both contestants on vocal rate
- 6 3. Shows that vocal rate does not conform to a mutual assessment process
- 7 4. Results show that fallow deer vocal rate follows an opponent-only process
- 8 5. Results do not conform to traditional assumptions concerning the function of vocal rates during ungulate contests

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